

Inventory of Japanese sacoglossan opisthobranchs: Historical review, current records, and unresolved issues

Cynthia D. Trowbridge^{1,*}, Yayoi M. Hirano², and Yoshiaki J. Hirano²

¹ Oregon Institute of Marine Biology, Charleston, Oregon, U.S.A.

² Department of Biology, Graduate School of Science, Chiba University, Japan

Correspondence, C. D. Trowbridge: cdt@uoregon.edu

Abstract: In the past ~155 years, professional and amateur malacologists have recorded *ca.* 90 described species of sacoglossan opisthobranchs in ~25 genera on Japanese shores. In addition, there are at least 20 to 40 undescribed or unrecognized sacoglossans also recorded. The extraordinary species richness has been a source of admiration as well as vexation. Worldwide scientific excitement in this group was largely due to two pivotal discoveries by Japanese researchers: (1) the acquisition and retention of functional chloroplasts by the sacoglossan *Elysia atroviridis* Baba, 1955 and (2) the existence of extant populations of bivalved sacoglossans (initially *Tamanovalva limax* Kawaguti and Baba, 1959 and then related taxa). Eight of the nine sacoglossan families recognized by Jensen (1996, 2007) are represented in Japan. All the recognized sacoglossan genera are represented in Japan except: *Roburnella* Marcus, 1982; *Platyhedyle* Salvini-Plawen, 1973; *Gascoignella* Jensen, 1985; *Olea* Agersborg, 1923; *Limapontia* Johnston, 1836; and the Australian genera *Edenttellina* Gatliff and Gabriel, 1911 and *Midorigai* Burn, 1960. Taxonomic uncertainty has been caused by the absence of vouchers, incomplete and/or questionable descriptions, photographic misidentifications (books and internet), chronically unstable classification, and other scientific challenges; in particular, the small size, cryptic coloration, and patchy distribution of sacoglossans have contributed to limited collections of many species. Since 2000, we have collected, photographed, and preserved unusually large numbers of Japanese sacoglossans, including species traditionally considered rare by malacologists. Although it is premature to produce a comprehensive inventory of the Japanese sacoglossan fauna, we consider it necessary to describe explicitly the strengths and weaknesses of current information. This assessment should assist professional and amateur malacologists with future sacoglossan study, particularly in the areas of biogeography, phylogeny, and ecology.

Key words: biodiversity, ecology, kleptoplasty, Sacoglossa, species richness

Biogeographic patterns of species richness (*i.e.*, the number of species) exhibit broad-scale patterns along latitudinal gradients and among ocean basins; these patterns are robust across large numbers of taxonomic groups of plants and animals. Understanding the evolutionary and ecological processes producing and maintaining such patterns of biodiversity is a central objective of evolutionary ecology and phylogeny. The comprehensive investigation of species-rich areas or “hot-spots” will enhance our understanding of the role that biotic factors play in structuring communities. In marine communities, Indo-Pacific and Western Pacific shores are characterized by an extraordinary number of species.

Within the gastropod order (or clade) Sacoglossa, species richness values vary geographically by up to two orders of magnitude (see Jensen 2007). Low values are recorded for North Atlantic shores: 3 species for the Black Sea (Martynov *et al.* 2007), 5 for New England (Clark 1975), and 9 for the British Isles (Thompson 1988). In the NE Pacific region, there are at least 25 sacoglossan species from Alaska to the equator (Trowbridge 2002). Comparable information for the western

Pacific, however, has been more problematic. There are at least 42 sacoglossan species on the Great Barrier Reef, 94 in the Marianas Islands, and *ca.* 80 in the Ryukyu Islands (Marshall and Willan 1999, Carlson and Hoff 2003, Ono 2004). Gosliner *et al.* (2008) recently reported *ca.* 107 sacoglossan species (including described and undescribed ones) for the Indo-Pacific region.

With the proliferation of local and regional web sites and photographic guides, it has become necessary to synthesize records for the western Pacific, particularly Japan which spans ~30° of latitude. When Baba (1937b) summarized opisthobranchs, there were only 9 species of sacoglossans recorded for Japan (Fig. 1). Spanning a range from 20° to 50°N latitude, Japanese shores are influenced by warm and cold-water currents that shape the opisthobranch fauna. Baba (1937b) suggested that the biogeographical break point of the warm- and cold-water fauna was around Akkeshi Bay on the Pacific shore of Hokkaido. Yet there have been only a few studies of sacoglossans from Hokkaido northward to the Kurile Islands or within the Sea of Japan (Baba 1935, Martynov

* Mailing address: P.O. Box 1995, Newport, Oregon 97365, U.S.A.

The rapid rate of sacoglossan species discovery and/or description has continued (Fig. 1), particularly due to the recent popularity of scuba diving, underwater photography, and internet slug sites. Ono (1999, 2004), Suzuki (2000), and Nakano (2004) have contributed immensely to the discovery of unknown sacoglossan species as well as the photographic documentation of described ones. Their efforts have been extremely valuable to amateur and professional malacologists. Ono's association with opisthobranch taxonomists at California Academy of Sciences has ensured that there are voucher specimens for most species and these are accessible to opisthobranch taxonomists. Ono's effect—particularly in conjunction with Gosliner (1995), Gosliner *et al.* (2008), Bolland (Okinawa Slug Site: <http://www.rfbolland.com/okislugs/>), and Rudman (Sea Slug Forum: <http://seaslugforum.net/>)—has been excellent. Ono has recorded a large number of Okinawan sacoglossans previously unknown from Japan.

There have been numerous other important malacologists (particularly Gosliner and Jensen) who formally described or redescribed sacoglossans that are now known to occur in Japan (Fig. 2). The actual records of collection of these species in Japan, however, are primarily from Ono (1999, 2004), Suzuki (2000), Nakano (2004), Bolland (Okinawa Slug Site), or others (on the Sea Slug Forum or various Japanese slug sites such as <http://www.umiushi.info>). For example, the first Japanese report of *Stiliger aureomarginatus* Jensen, 1993 was made by Suzuki (2000). Furthermore, Nakano (2004) published the first photograph of *Calliopaea pusillus* (Baba, 1959) (as *Stiliger pusillus* Baba, 1959); internet records may have preceded Nakano's printed record.

Authors

Trowbridge, Hirano, and Hirano have been collecting Japanese sacoglossans together since 2000. Voucher specimens have been deposited at Chiba University in the extensive Hirano opisthobranch collection. High-resolution photographic vouchers of species have been made during each collecting trip. Because our taxonomic work is currently in progress, we emphasize records pre-dating our research. Also, as many sacoglossans are undescribed (or perhaps just unrecognized) in Japan and elsewhere (Fig. 3), we consider the present paper to be an interim inventory—though an essential one—of Japanese species.

Shelled sacoglossans

Single-valved species

Although shelled sacoglossans are now known to be widely distributed and often abundant, these taxa have traditionally been considered rare. On Japanese shores, the single-shelled species (the oxynoids and volvatellids) have been known for many decades. Prof. Tadashige Habe described

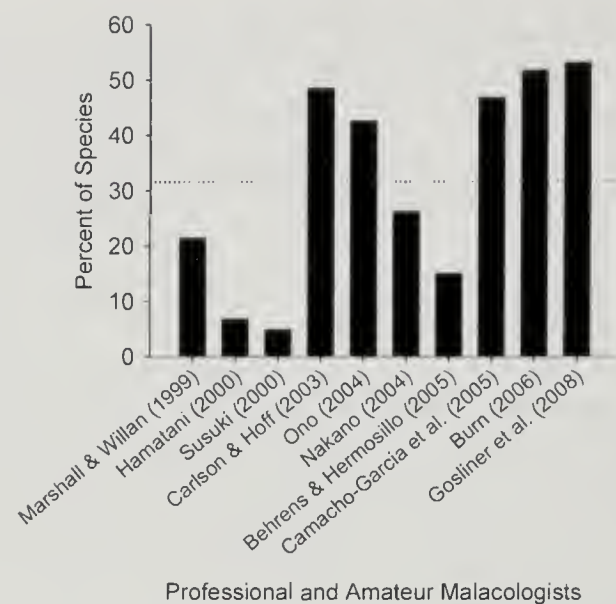


Figure 3. The estimated percentage of sacoglossan species that are unidentified—either undescribed or unrecognized—in several recent field or literature surveys of opisthobranchs. As several authors present taxa as species complexes, these values are inherently estimates. The dotted horizontal line represents the mean value of unidentified species.

Volvatella kawamurai Habe, 1946 and provided the first report of *Oxynoe* in Japan (Habe 1946, 1949). As mentioned in the previous section, Hamatani described four shelled species (*Ascobulla japonica*, *Volvatella ayakii*, *Volvatella viridis*, and *Oxynoe kabirensis*) and Ichikawa described one (*Volvatella angeliniana* Ichikawa, 1993). Kitao (1979) published descriptions of the veliger larvae of a Japanese *Volvatella* and *Oxynoe*.

Bivalved species

In terms of bivalved sacoglossans (Juliidae), Kuroda (1935a, 1935b) first reported shells of *Julia exquisita* (Gould, 1862); however, these two early reports listed the species as a member of the bivalve family Ungulinidae. It was only when the living bivalved sacoglossans were discovered that they were reassigned to the opisthobranch gastropods: Kuroda and Habe (1951) described *Julia japonica*, a small but frequent species. Extant populations of Juliidae and aspects of their intriguing biology were described by Kawaguti (1959, 1982), Kawaguti and Baba (1959), Kawaguti and Yamasu (1959, 1960a, 1960b, 1960c, 1961a, 1961b, 1962, 1966a, 1966b, 1967), Baba (1961a, 1961b), Kitao (1978), and Yamasu (1997). The records of *Tamanovalva limax* (called *Berthelinia limax* by many but not all malacologists) and subsequently *Julia* spp. (Kawaguti and Yamasu 1962, 1982, Yamasu 1968, 1969, Kawaguti 1981) stimulated the international research community immensely. For example, Cox and Rees (1960) published a *Nature* commentary of the paper of Kawaguti and Baba (1959), highlighting the discovery of the live specimens

and the recognition that these bivalved species are actually gastropods. Soon reports of bivalved sacoglossans were made from Hawaii (Kay 1962a, 1962b, 1968), California (Keen 1960, Keen and Smith 1961, Smith 1961), Jamaica (Edmunds 1962, 1963), Australia (Burn 1960a, 1960b, 1960c), and India (Rao 1965, Ganapati and Sarma 1972, Sarma 1975).

Although some researchers have suggested referring to all Pacific *Julia* specimens as *Julia exquisita* (Gould, 1862), this advice was based on the erroneous assumptions that specimen numbers were insufficient for study and that detailed anatomical work had not yet been done. We take the conservative approach of retaining the described names, particularly given our knowledge of extensive unpublished Japanese work on this group (discussed below).

Anatomy, development, and field associations

In addition to stimulating international research, Kawaguti and Yamasu (together and individually) have produced an entire series of highly detailed papers on the internal anatomy of *Tamanovalva limax*, *Julia japonica*, and others. These morphological papers—with the addition of ones by Kawaguti (1941, 1968), Kawaguti *et al.* (1965), Baba and Hamatani (1970a, 1970b), Baba (1986), Adachi (1991), Hirose (2005), and Hirano *et al.* (2006b, 2007c, 2008a, 2008b, 2009, 2010a, 2010b)—are the only detailed accounts of Japanese sacoglossan anatomy. Thus, the extraordinary diversity of sacoglossans in Japan has not yet been accompanied by extensive anatomical work. There is a pressing need for anatomical and developmental work of Japanese species comparable to the excellent standard set by Kawaguti, Yamasu, and colleagues.

From 1986 to 1991, at least six students at the University of Ryukyus in Okinawa investigated sacoglossans (T. Iseto, pers. comm.). For example, the development of *Julia* and *Tamanovalva* were studied by Sato (1986), Chibana (1987), and Iseto (1996); the comparative morphology of Juliidae was investigated by Mizofuchi (1987, 1990) and Murayama (1989). Intriguingly, Mizofuchi (1990) compared *Berthelinia* and 5 *Julia* species—1 species more than reported by more recent amateur or professional malacologists. To our knowledge, the wealth of Okinawan research on these bivalved sacoglossans has not yet been published within the Japanese or international literature with the exception of tantalizing abstracts (Mizofuchi and Yamasu 1987, Yamasu and Adachi 1990). However, Iseto (pers. comm.) indicated he would publish a synthesis of those.

Our group's success in locating shelled sacoglossans in Okinawa was a direct result of the valuable and detailed collection advice of Prof. Yamasu shortly before our survey program started. For example, in six brief visits to Okinawa from July 2002 to March 2005, we found Volvatellidae (5 *Volvatella* spp., 49 specimens), Oxynoidae (3 species, 37 speci-

mens), and Juliidae (4 species, 8 specimens). The perception that these species are unusual or rare is not strictly true. In fact, Mizofuchi and Yamasu (1987: 1112) reported that “Several hundred living specimens of genus *Julia* were collected ... in 1986 and 1987.” Yamashita *et al.* (1998) found six live *Julia* specimens on a single day on Tsunoshima Island, NW Yamaguchi Prefecture, Japan. Finally, Kawaguti and Yamasu (1982) collected 13 live specimens of *J. japonica* at Tsunoshima and ca. 20 from Ishigaki Island in Okinawa.

Self-fertilization

The report of self-fertilization in a bivalved sacoglossan (Kawaguti and Yamasu 1961a) also intrigued malacologists. Although all sacoglossans are hermaphroditic, self-fertilization has been described in only two other cases of the other hundreds of species worldwide. The Atlantic *Berthelinia caribbea* Edmunds, 1963 produces offspring without mating (Grahame 1969) and the NE Pacific *Alderia willowi* Krug *et al.*, 2007 does as well (Smolensky *et al.* 2009). The latter study explored the costs of mating, particularly given the species' hypodermic insemination, in an elegant series of controlled experiments.

Kleptoplasty or chloroplast retention

Initial discovery

One of the major contributions of Japanese sacoglossan researchers is the discovery that ingested algal chloroplasts were retained within sacoglossan digestive diverticulae. This phenomenon—now called kleptoplasty—was described by Kawaguti and Yamasu (1965) in reference to *Elysia atroviridis* Baba, 1955 associated with the green alga *Codium fragile*. Kawaguti (1941) and Kawaguti *et al.* (1965) also investigated *Plakobranthus* but the system was not understood as well as the *Elysia* one (e.g., retained algal chloroplasts were interpreted as unicellular algae). Extensive work (well-reviewed elsewhere) was subsequently conducted by European workers on the ecological analog of *E. atroviridis*, namely *Elysia viridis*, of NE Atlantic shores, particularly the functionality of the retained chloroplasts and their role in the energetics of the slugs. Despite the discovery of the concept of kleptoplasty, researchers have not yet characterized the frequency with which it occurs within the diverse sacoglossan group on Japanese shores.

Pulse amplitude modulated fluorometry (PAM)

A new method, namely the use of PAM to characterize the functionality of ingested chloroplasts, shows great potential in characterizing Japanese species. Sue Williams (2000a, 2000b) used PAM and mass spectrometry to investigate the photobiology of Australasian sacoglossans for her

Ph.D. research at University of Western Australia at Perth; the methodology was subsequently used by Evertsen *et al.* (2007), Grzybowski *et al.* (2007), and Händeler *et al.* (2009, 2010) for a suite of Indo-Pacific and Mediterranean species, several of which also occur in Japan. This methodology was recently employed by Yamamoto *et al.* (2008, 2009) to investigate Japanese sacoglossans; they found photosynthetically active chlorophyll in *ca.* 8–10 species in five families. This research group is continuing their work on functional kleptoplasty in Japanese sacoglossan assemblages (Yamamoto, pers. comm.).

Molecular approaches

Several research groups have started using molecular techniques to identify the retained algal chloroplasts within sacoglossan tissues. The methodology, first described by Curtis *et al.* (2006, 2007) for Florida sacoglossans, is being employed by the research groups of Dr. Tadashi Maruyama and Prof. Euichi Hirose in Japan. For example, for his Ph.D. research, Taro Maeda is investigating chloroplast retention in *Plakobranchius ocellatus* van Hasselt, 1824 (*sensu lato*) and using molecular tools to identify the algal hosts (Maeda *et al.* 2009). Maeda (2009) discussed whether genes involved in photosynthesis are transferred from algal host to sacoglossans.

Ecological research

Field populations

Numerous researchers have recorded algal host associations of sacoglossan herbivores on the shore. However, quantitative ecological work rigorously investigating feeding preferences, diet breadth, and host-use has only recently been initiated (*e.g.*, Usuki 1977, Hirano and Hirano 1991, Shimadu 2005, Shimadu *et al.* 2006, Hirano *et al.* 2007b, Kumagai *et al.* 2008, Trowbridge *et al.* 2005, 2006, 2008a, 2008b, 2009a, 2009b, 2009c, 2010a, 2011, Kumagai 2009). Population studies of Japanese sacoglossans are meager (but see Usuki 1977, Hirose *et al.* 2003, Shimadu 2005, Shimadu *et al.* 2006, Trowbridge *et al.* 2008a, 2008b, 2009a, 2009b, 2010a, 2010b, 2010c, 2011, and Kumagai 2009 for notable exceptions). Usuki's research was particularly noteworthy because it was both quantitative and comparative; Usuki compared the ecology of *Ercolania boodleae* (Baba, 1938) to its European and North American analogs feeding on filamentous green algae. Quantitative life-history attributes of *Tamanovalva limax*, including life span, were also characterized by Kawaguti and Yamasu (1960b).

Reproductive ecology

Detailed descriptions of spawn masses, egg and capsule sizes, and veliger larvae have been made by Baba *et al.* (1956), Hamatani (1960, 1963, 1967), and Kitao (1979).

Characterization of spawn masses, embryos, and larval type (planktotrophic and lecithotrophic) of all Japanese sacoglossans is currently in progress by the authors of the present paper. Quantitative larval ecology of Japanese sacoglossans has not yet been endeavored despite the diversity of species. Given that the majority of the sacoglossans have long-lived planktonic larvae, the paucity of study is understandable; few such species have been cultured through their life cycles. Understanding the breadth of larval choice among sympatric host and non-host algae would enable us evaluate how frequently sacoglossans are extreme specialists (*e.g.*, monophagous herbivores) vs. less stenophagous ones. Larval work on the European *Elysia viridis* demonstrated (Trowbridge and Todd 2001) that sacoglossans can have much broader metamorphic cues than traditionally presumed: the adult food is not the sole metamorphic trigger, in contrast to what has traditionally been presumed.

Diet breadth

Recent work on *Codium*-feeding sacoglossans on Honshu demonstrated that the high diversity of *Codium* spp. (*ca.* 20) is attacked by slugs. Monophagy (*i.e.*, extreme specialization) was not found in the high-diversity temperate systems (Trowbridge *et al.* 2009a) or in subtropical Okinawan ones (Trowbridge *et al.* 2010c). The generality of these results to the *Caulerpa*-feeding species remains to be seen but is under current investigation by the authors.

Current topics

Three fields of sacoglossan ecology currently being investigated are parasites, competitors, and predators. Kosuke Sudo at Chiba University has been characterizing the frequency and identity of parasites. Sudo (2005, 2007) and Sudo *et al.* (2005, 2007, 2008, 2009, 2010, 2011) described splanchnotrophid copepods and turbellarian flatworms that parasitize four and six species of sacoglossans, respectively, on the Pacific shores of Honshu. Additional parasite records have been noted for Okinawa and Kyushu (Sudo, pers. comm.). Sudo repeatedly found both types of parasites, sometimes abundantly, from at least a few to several sacoglossan species (Sudo *et al.* 2010, 2011). Sudo's research shows that investigating parasite-host interactions merits further study as a generally overlooked, but potentially important, interaction.

Trowbridge *et al.* (2009a) evaluated the nature of interspecific interactions of sympatric sacoglossan species—competition, facilitation, or no interactions. Field observations and laboratory experiments indicated there was no evidence of competition or facilitation among coexisting species on *Codium* in Sagami Bay, Honshu.

Finally, in Okinawa, Nakano *et al.* (2007) have documented the feeding of *Gymnodoris* Stimpson, 1855 on other opisthobranchs: sacoglossans are among the prey species. Based

on this Japanese work and earlier research on NE Pacific and NE Atlantic shores (Trowbridge 1994 and unpubl. data), sacoglossan predators include some fishes, birds, crabs, nudibranchs, and mites. Because sacoglossans dwell within marine communities, there is real need to understand the interspecific and intraspecific interactions of the species rather than just the sacoglossans (in isolation) or the sacoglossan-algal interactions (without other interacting species) as traditionally investigated.

KNOWN TAXA

Classification systems

Baba (1937b: 195) remarked that: “The classification and nomenclature of the Opisthobranchia are serious problems still not satisfactorily resolved. Subsequent investigations therefore will render it necessary to alter some of the accounts of the species, genera or even families contained in this paper.” These words accurately reflect the taxonomic uncertainty still plaguing sacoglossan researchers today. Jensen (1996) has shown the validity of sacoglossan families. Recent molecular work [including Bass and Karl (2006), Händeler and Wägele (2007), Händeler *et al.* (2009), Maeda *et al.* (2010), and Krug *et al.* (in progress)] have partly confirmed the validity of some families and genera. Our present account does not establish new taxonomic considerations but rather will bridge the gap between species’ initial records on Japanese shores and the currently used names and systematic arrangement.

Families, genera, and species

All 3 families of suborder Oxynoacea are represented in Japan: Volvatellidae, Juliidae, Oxynoidea. Of suborder Plakobranchacea, 5 of the 6 families are represented: Plakobranchidae, Bosellidae, Polybranchiidae, Hermaeidae, and Limapontiidae but not Platyhedylidae.

Of the 31 sacoglossan genera recognized by Jensen (1996), 25 have been reported from Japan (Table 1). The only sacoglossan genera not yet reported from Japan are *Roburnella* Marcus, 1982 (Oxynoidae); *Platyhedyle* Salvini-Plawen, 1973 and *Gascoignella* Jensen, 1985 (Platyhedylidae); *Olea* Agersborg, 1923 and *Limapontia* Johnston, 1836 (Limapontiidae); and *Edenttellina* Gatliff and Gabriel, 1911 and *Midorigai* Burn, 1960 (Juliidae). However, the validity of several genera has been questioned so the precise genus count is controversial.

The number of described sacoglossan species recorded from Japanese shores is about 90 (Table 1) while the number of recognized species exceeds 100; the total number—including undescribed species recognized by Carlson and Hoff (2003), Ono (2004, 2005), Gosliner *et al.* (2008), and our research group—will probably be *ca.* 125–140 sacoglossan species. The degree of uncertainty is a direct result of the high

percentage (*ca.* 32%) of unidentified sacoglossan species (Fig. 3), either undescribed cryptic species or unrecognized ones. By unrecognized species, we refer to those species for which authors have not assigned a species name. As many of the Japanese sacoglossans are broadly distributed Indo-Pacific species, we adopt the conservative approach of comparing our species to all congeners described (worldwide) before presuming our species are local endemics and describing them as such. Several of Baba’s described species were subsequently synonymized with Indo-Pacific congeners. Given the challenges of finding the full citations of type descriptions of sacoglossans, many professional and amateur malacologists publish their records as unidentified species.

Malacologists are still on the steep part of the species and genus accumulation curves (Fig. 1). The rapid rate of species discovery and/or description has continued, particularly due to the recent popularity of scuba diving, underwater photography, and internet slug sites. Although photographic identifications often are challenging, the misidentifications made are understandable given the difficulty in distinguishing some species.

THE CHALLENGES

There is still considerable taxonomic controversy regarding several family, genus, and species names. At the family level, we follow the classification system of Jensen (1996) while acknowledging the existence of alternate systems currently in use on the *Sea Slug Forum* (Australian Museum) and by Valdés and Bouchet in Bouchet and Rocroi (2005). Until molecular studies fully elucidate the relationships of genera, there will be ongoing disagreement among colleagues about sacoglossan classification. Maeda (2007) investigated the molecular phylogeny of the Sacoglossa for his M.Sc. thesis. This work (Maeda *et al.* 2006, 2010) complements ongoing research by two other research groups (Patrick Krug at California State University in Los Angeles; Heike Wägele at the University of Bonn in Germany).

At the genus level, there continues to be a lack of consensus about the status of: (1) *Pattyclaya* Marcus, 1982 and *Elysiella* Verrill, 1872 and (2) *Tamanovalva*, *Berthelinia*, *Edenttellina*, and *Midorigai*. Molecular and cladistic evidence supports the elimination of *Elysiella* as the species fall within the clade of *Elysia* (Gosliner 1995, Bass and Karl 2006, Händeler and Wägele 2007, Händeler *et al.* 2009); comparable information is needed for *Pattyclaya*. With respect to the bivalved taxa, continued uncertainty or disagreement includes the proper genus name for *Tamanovalva limax* and *Berthelinia schlumbergeri* Dautzenberg, 1895 (*e.g.*, Baba 1961a, 1961b, Rudman 2001e, 2002b). Opisthobranch taxonomists and other researchers are still divided on the use of the same genus name (*Berthelinia* Crosse, 1875) for extinct and extant species

Table 1. List of all described sacoglossan species recorded from Japanese shores. Citations of taxonomic authorities are listed in the literature-cited section. Notes are summarized in Appendix 1.

Family	Species	Authority	Notes
Volvatellidae	<i>Ascobulla japonica</i>	(Hamatani, 1969)	
	<i>Volvatella angeliniana</i>	Ichikawa, 1993	
	<i>Volvatella ayakii</i>	Hamatani, 1972	
	<i>Volvatella kawamurai</i>	Habe, 1946	
	<i>Volvatella vigourouxii</i>	(Montrouzier in Souverbie, 1861)	1
	<i>Volvatella viridis</i>	Hamatani, 1976	2
Oxynoidae	<i>Lobiger souverbii</i>	Fisher, 1856	3
	<i>Lobiger viridis</i>	Pease, 1863	4
	<i>Oxynoe kabirensis</i>	Hamatani, 1980	
	<i>Oxynoe viridis</i>	(Pease, 1861)	
Juliidae	<i>Berthelinia schlumbergeri</i>	Dautzenberg, 1895	5
	<i>Julia exquisita</i>	(Gould, 1862)	
	<i>Julia japonica</i>	Kuroda and Habe, 1951	6
	<i>Julia mishimaensis</i>	Kawaguti and Yamasu, 1982	
	<i>Julia zebra</i>	Kawaguti, 1981	7
	<i>Tamanovalva limax</i>	Kawaguti and Baba, 1959	8
Plakobranchidae	<i>Elysia abei</i>	Baba, 1955	9
	<i>Elysia amakusana</i>	Baba, 1955	10
	<i>Elysia atroviridis</i>	Baba, 1955	11
	<i>Elysia babai</i>	Pruvot-Fol, 1946	12
	<i>Elysia beunetiae</i>	Thompson, 1973	13
	<i>Elysia cf. tomentosa</i>	Jensen, 1993	14
	<i>Elysia flavipunctata</i>	Ichikawa, 1993	15
	<i>Elysia hamatanii</i>	Baba, 1957	
	<i>Elysia hirasei</i>	Baba, 1955	16
	<i>Elysia japonica</i>	Eliot, 1913	17
	<i>Elysia lobata</i>	Gould, 1852	18
	<i>Elysia mercieri</i>	(Pruvot-Fol, 1930)	
	<i>Elysia minima</i>	Ichikawa, 1993	19
	<i>Elysia nigrocapitata</i>	Baba, 1957	
	<i>Elysia obtusa</i>	Baba, 1938	20
	<i>Elysia ornata</i>	(Swainson, 1840)	21
	<i>Elysia pusilla</i>	(Bergh, 1872)	22
	<i>Elysia rufescens</i>	(Pease, 1871)	23
	<i>Elysia setoensis</i>	Hamatani, 1968	24
	<i>Elysia sugashimae</i>	Baba, 1955	25
	<i>Elysia thompsoni</i>	Jensen, 1993	26
	<i>Elysia trisinuata</i>	Baba, 1949	27
	<i>Elysia yaeyamana</i>	Baba, 1936	28
	<i>Elysiobranchus ryukyuensis</i>	Ichikawa, 1993	29
	<i>Pattyclaya arena</i>	Carlson and Hoff, 1977	30
	<i>Plakobranchus ocellatus</i>	van Hasselt, 1824	31
	<i>Thuridilla albopustulosa</i>	Gosliner, 1995	
	<i>Thuridilla bayeri</i>	(Marcus, 1965)	32
	<i>Thuridilla carlsoni</i>	Gosliner, 1995	

Table 1. (continued)

Family	Species	Authority	Notes
	<i>Thuridilla flavomaculata</i>	Gosliner, 1995	
	<i>Thuridilla gracilis</i>	(Risbec, 1928)	33
	<i>Thuridilla hoffae</i>	Gosliner, 1995	
	<i>Thuridilla kathae</i>	Gosliner, 1995	
	<i>Thuridilla livida</i>	(Baba, 1955)	
	<i>Thuridilla splendens</i>	(Baba, 1949)	
	<i>Thuridilla undula</i>	Gosliner, 1995	
	<i>Thuridilla vatae</i>	(Risbec, 1928)	
Polybranchiidae/Caliphyllidae	<i>Cyerce kikutarobabai</i>	Hamatani, 1976	
	<i>Cyerce nigricans</i>	(Pease, 1866)	
	<i>Mourgona osumi</i>	Hamatani, 1994	
	<i>Polybranchia orientalis</i>	(Kelaart, 1858)	
	<i>Sohgenia palauensis</i>	Hamatani, 1991	
Limapontiidae	<i>Alderia modesta</i>	(Lovén, 1844)	34
	<i>Alderiopsis nigra</i>	(Baba, 1937)	34
	<i>Aplysiopsis minor</i>	(Baba, 1959)	
	<i>Aplysiopsis nigra</i>	(Baba, 1949)	
	<i>Aplysiopsis orientalis</i>	(Baba, 1949)	
	<i>Aplysiopsis toyamana</i>	(Baba, 1959)	
	<i>Calliopaea pusillus</i>	(Baba, 1959)	35
	<i>Costasiella formicaria</i>	(Baba, 1959)	
	<i>Costasiella iridophora</i>	Ichikawa, 1993	
	<i>Costasiella kuroshimae</i>	Ichikawa, 1993	
	<i>Costasiella paweli</i>	Ichikawa, 1993	
	<i>Costasiella rubrolineata</i>	Ichikawa, 1993	
	<i>Costasiella usagi</i>	Ichikawa, 1993	
	<i>Costasiella vegae</i>	Ichikawa, 1993	36
	<i>Ercolania kencolesi</i>	Grzybowski <i>et al.</i> , 2007	37
	<i>Ercolania boodlea</i>	(Baba, 1938)	
	<i>Ercolania coerulea</i>	(Trinchese, 1893)*	
	<i>Ercolania subviridis</i>	(Baba, 1959)	38
	<i>Hermaea noto</i>	(Baba, 1959)	39
	<i>Hermaea vancouverensis</i>	O'Donoghue, 1924	40
	<i>Hermaea wrangeliae</i>	(Ichikawa, 1993)	41
	<i>Hermaea zosterae</i>	(Baba, 1959)	39
	<i>Placida cremoniana</i>	(Trinchese, 1893)*	
	<i>Placida daguilaensis</i>	Jensen, 1990	
	<i>Placida</i> sp. (<i>sensu</i> Baba 1986)**	Baba, 1986	42
	<i>Stiliger aureomarginatus</i>	Jensen, 1993	
	<i>Stiliger berghi</i>	Baba, 1937	43
	<i>Stiliger ornatus</i>	Ehrenberg, 1828	
	<i>Stiliger smaragdinus</i>	Baba, 1949	44

* not 1892 as stated by many authors (books, papers, and internet)

** described but not named

because the hypothesis of convergent shell shape cannot be refuted.

At the species level, there persists the concern of whether certain taxa are species complexes or single, phenotypically

variable species. Problematic "species" include *Placida dendritica* reported for Japan (Baba 1937b), redescribed by Marcus (1982), and then again by Baba (1986). Bleakney (1989) prematurely synonymized many *Placida* spp. from

Table 2. List of undescribed but recognized sacoglossan species recorded from Japanese shores. Our unpublished data are preliminary estimates.

Families	Genera	Bolland (<i>Okinawa Slug Site</i>)	Hamatani (2000)	Ono (2004)	Nakano (2004)	Hirano <i>et al.</i> (unpubl. data)
Volvatellidae	<i>Volvatella</i>	2				1-2?
Bosellidae	<i>Bosellia</i>	1		1	1	1
Plakobranthidae	<i>Elysia</i>			12	7	11-12?
	<i>Pattyclaya</i>		1			
	<i>Plakobranthius</i>		1			4-5
	<i>Thuridilla</i>			1		
	<i>Caliphylla</i>					1
Polybranchiidae/Caliphyllidae	<i>Cyerce</i>	2		5	4	
	<i>Polybranchia</i>					2
	<i>Soligenia</i>			1		1
	<i>Aplysiopsis</i>	1				
Limapontiidae	<i>Costasiella</i>	3		3		2-3
	<i>Ercolania</i>	2		7	1	7-8?
	<i>Hermatea</i>	4		3	1	
	<i>Placida</i>	1				1-2
	Total	16	2	33	14	31-37

temperate shores around the world based almost exclusively on radular tooth morphology but did not present any reproductive comparisons or other morphological features. Hirano *et al.* (2006a, 2006c) clarified several of the cryptic Japanese species attributed to the name *P. dendritica*. Shimadu (2005), Shimadu *et al.* (2006), Kumagai *et al.* (2008), and Kumagai (2009) reported ecological and morphological work on *Placida* sp. (*sensu* Baba 1986). In fact, Gosliner *et al.* (2008: 72) noted that “Many members of this genus have been lumped under the name *Placida dendritica*, but different populations have distinctive branching patterns of the digestive gland and probably represent a complex of distinct species.” Martynov (2006) also illustrated two “forms” of *P. dendritica* with different branching patterns on Russian shores; he suggested they may be seasonal ecotypes (summer vs. winter forms) or separate species (Martynov, pers. comm.).

A second example is the long-term controversy regarding the number of *Plakobranthius* spp. occurring in Okinawan waters as well as circum-tropical regions worldwide. *Plakobranthius guttatus* was described by Stimpson (1855) but Baba (1936) synonymized this species with *P. ocellatus*. Yamasu and Adachi (1990), Adachi (1991), Yamasu (1997), Hirano *et al.* (2005), and Ono (2005) have all remarked on the 4-5 types or morphs of *P. ocellatus* in Okinawa and hypothesized that the taxon is actually a complex of sibling species. Furthermore, Hamatani (2000) recognized two species. Based on external coloration (authors’ unpubl. data on >1000 specimens from Okinawa), population dynamics, development, and genetic differences (P. Krug, pers. comm.),

there are multiple distinct species being recognized under the name *P. ocellatus* in Japan. The species boundaries have not yet been fully established but are currently in progress.

As the Japanese fauna becomes more studied, some of the species originally considered to be endemic to Japan are being synonymized with other, particularly Indo-Pacific species. Recent examples include (1) *Elysia kushimotoensis* Baba, 1957, now considered to be *E. rufescens* (Pease, 1871) and (2) *Elysia tokarensis* Baba, 1957, now considered to be *E. lobata* Gould, 1852 (e.g., Nakano 2004, Ono 2004). Both of these synonymies were based on photographs with no published records of anatomical comparisons or acknowledgment of detailed published descriptions of the Japanese species (e.g., Kitao 1977). Another example is the suggested or stated synonymy of *Elysia obtusa* Baba, 1938 and *Elysia flava* Verrill, 1901 (e.g., Rudman 2001a, Gosliner *et al.* 2008, and many internet sites). Although the first two suggested synonymies are seemingly not controversial, the third one is problematic as it involves a Pacific and an Atlantic species. With scientists’ recent focus on introduced species, are we prematurely considering species to be conspecific based on external similarity alone despite known biogeographical boundaries? [For example, see discussion on *Sea Slug Forum* about *Bosellia* from the western Pacific (Rudman 2004)]. Although photographic comparisons and informal, online discussions are informative, they are not sufficient, by themselves, for taxonomic synonymies. Morphological, reproductive, and genetic evidence should still be rigorously evaluated particularly in the high-diversity, but largely unexplored, group.

TYPE DESCRIPTIONS

Given the current journal publication convention not to list the citation details of type descriptions, the valuable details necessary to verify sacoglossan species are becoming extremely difficult to locate. In larger groups such as nudibranchs, researchers have compiled and published bibliographies and full citations of type descriptions (e.g., McDonald 2009a, 2009b). To ensure that such crucial sacoglossan information is preserved for future malacologists, we have included the citations of the original descriptions of Japanese sacoglossans (Appendix 2).

CONCLUSIONS

There is a wealth of information in Japanese that is relatively inaccessible to and/or unrecognized by most non-Japanese malacologists. For example, many of the journals are not electronically indexed so citations do not appear in electronic databases used in the U.S., Europe, etc. Our brief review of the scope and details of Japanese contributions should facilitate and enhance the study of sacoglossan research worldwide. There are pressing needs to investigate (1) shelled sacoglossan species and both *Ercolania* and *Placida* species complexes; (2) the population ecology and ecological role of sacoglossans; (3) the role of genetics and development in determining host choice; and (4) speciation on the high-diversity but taxonomically challenging shores of Japan and environs.

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Appendix 1. Explanatory notes relating to described sacoglossan species listed in Table 1.

#	Notes
1	Rudman (2002f)
2	Rudman (2002e)
3	<i>Lobiger souverbii</i> is the correct spelling and this species is synonymous with <i>L. sagamiensis</i> Baba, 1952 (Baba 1974, Rudman 2000c, 2001c).
4	Rudman (2001c)
5	Genus name controversial (Rudman 2002b).
6	May be synonymous with <i>J. zebra</i> ; but see Kitao (1978).
7	May be synonymous with <i>J. thecaphora</i> Carpenter, 1857 (Pittman 2001).
8	Genus name controversial (Rudman 2001e, 2002b).
9	The questionable distinction between this species and <i>E. amakusana</i> was acknowledged in its description (Baba 1955a); both are now considered color morphs of <i>E. abei</i> (Rudman 2002g).
10	The questionable distinction between this species and <i>E. abei</i> was acknowledged in its description (Baba, 1955b); both are now considered color morphs of <i>E. abei</i> (Rudman 2002g).
11	Genetically indistinguishable from <i>E. setoensis</i> (A. Bass, pers. comm.; P. Krug, pers. comm., different specimens).
12	Never recorded since its description: Baba (1936) reported <i>E. viridis</i> from Okinawa but the radular teeth are extremely different from those of the European species; consequently, Pruvot-Fol renamed the Okinawan species <i>E. babai</i> Pruvot-Fol, 1946. However, there have been no subsequent records of this species so its identity is unclear.
13	Controversial about this species' identity and features differentiating it from <i>Elysia yaeyamana</i> (Carlson and Hoff 1978, 2003, Marshall and Willan 1999; Trowbridge, pers. obs.)
14	Species complex (Rudman 2001d, Ono 2004, P. Krug, unpubl. data); see Kitao (1976) for first published Japanese record.
15	Never recorded since its description.
16	Species recorded as <i>E. viridis</i> by Hirasé (1927), Baba (1949), Taki (1951); it then was redescribed as <i>E. hirasei</i> (Baba 1955a); also see (Rudman 2005c, 2009).
17	Type description too vague, no type locality information, and no voucher; Rudman suggests we abandon the species name (Rudman 2002a, 2002g).
18	No published anatomical comparisons made to substantiate name change from <i>E. tokarensis</i> Baba, 1957 (see Rudman 2001b, Nakano 2004); for anatomy of Japanese specimens, see Baba (1957) and Kitao (1977).
19	Never reported since its description though we may have re-discovered it in April 2010.
20	May be synonymous with <i>E. flava</i> (Rudman 2001a, Gosliner <i>et al.</i> 2008) but controversial.
21	May be synonymous with <i>E. marginata</i> and <i>E. gaudifolia</i> (see Rudman 1999b, 2001b; Jensen 2001b) or may be a complex of cryptic species; molecular evidence supports the latter (P. Krug, unpubl. data).
22	<i>Elysiella</i> synonymized with <i>Elysia</i> (Gosliner 1995, Bass and Karl 2006, Händeler and Wägele 2007, Händeler <i>et al.</i> 2009, P. Krug, unpubl. data).
23	No external or internal anatomical comparisons made to support name change from <i>E. kushimotoensis</i> Baba, 1957 (see Rudman 1999a, 2002d).
24	Genetically indistinguishable from <i>E. atroviridis</i> (P. Krug, pers. comm.) but is morphologically distinct.
25	Synonymous with <i>E. trisinuata</i> : intraspecific variation in tooth shape (Trowbridge <i>et al.</i> 2006).
26	Ono (2004); Hirano <i>et al.</i> (unpubl. data)
27	Synonymous with <i>E. sugashimae</i> : intraspecific variation in tooth shape (Trowbridge <i>et al.</i> 2006).
28	Unclear about this species' identity and features differentiating it from <i>Elysia bennettiae</i> (Marshall and Willan 1999, Carlson and Hoff 2003, Trowbridge, pers. obs.).
29	Never recorded since its description; genus not recognized by all opisthobranch taxonomists.
30	May be <i>Elysia arena</i> ; validity of genus name is controversial (Rudman 2006a).
31	Species complex: at least 4-5 color morphs in Japan with at least 3 distinct species (Yamasu and Adachi 1990, Adachi 1991, Ono 2004, 2005, Trowbridge <i>et al.</i> , unpubl. data, P. Krug, unpubl. data).
32	Controversy of synonym (Rudman 2000a).
33	Controversy of synonym (Rudman 2000b).
34	Baba (1937a, 1968) described and redescribed the species <i>Alderia/Alderopsis nigra</i> . Nishina found some similar specimens; molecular evidence (P. Krug, pers. comm.) indicates these were <i>Alderia modesta</i> . Russian specimens of <i>A. modesta</i> have also been reported (Chernyshev and Chaban 2005, Rudman 2005a). However, <i>A. nigra</i> was recently discovered elsewhere and CDT confirmed the specimens; therefore, we consider Baba's specimens and Nishina's specimens are separate species.

Appendix 1. (Continued)

#	Notes
35	Genus name uncertain. Described as <i>Stiliger</i> by Baba (1959). Baba and Hamatani (1970a) suggested species belonged to <i>Calliopaea</i> ; no longer considered <i>Stiliger pusillus</i> as published by many amateurs.
36	Rudman (2006b)
37	Hirano <i>et al.</i> (2006d, 2007c, unpubl. research); also reported by Carlson and Hoff (2003).
38	Hirano <i>et al.</i> (unpubl. research), Rudman (2005b); <i>Ercolania subviridis</i> (Baba, 1959) may be the same as <i>Ercolania varians</i> (Eliot, 1904) reported by Carlson and Hoff (2003) in the Marianas. Eliot's type specimens have not been located.
39	<i>Hermaea noto</i> may be synonymous with <i>H. zosteræ</i> (Jensen 2000, Rudman 2002c) but the tooth counts are extremely different, indicative of separate species. <i>Hermaea noto</i> has 10 ascending + 38 descending teeth whereas <i>H. zosteræ</i> has 6 ascending + 13 descending ones.
40	Genus name and species identity uncertain: <i>Stiliger akkeshiensis</i> Baba, 1935 was described from Akkeshi Bay, Hokkaido. It appears that <i>S. akkeshiensis</i> refers to <i>Hermaea vancouverensis</i> O'Donoghue (1924) described from NE Pacific shores (Hirano <i>et al.</i> 2008a, 2008b). The Russian specimens recorded by Martynov for the Kuriles have been confirmed to be <i>H. vancouverensis</i> (see Rudman 2005d).
41	Original genus assignment (<i>Aplysiopsis</i>) incorrect; no vouchers and insufficient description (Trowbridge <i>et al.</i> 2009b).
42	See Hirano <i>et al.</i> (2006a, 2006b, 2006c).
43	Genus name uncertain: probably belongs to undescribed genus (Baba and Hamatani 1970a) or to <i>Hermaea</i> (Hirano <i>et al.</i> 2008a).
44	Genus name uncertain: probably belongs to undescribed genus (Baba and Hamatani 1970a, Jensen 2001a).

Appendix 2. Citations of type descriptions of Japanese sacoglossans. * denotes Japanese descriptions of species subsequently synonymized with Indo-Pacific ones.

- * Baba, K. 1935. The fauna of Akkeshi Bay. I. Opisthobranchia. *Journal of the Faculty of Science, Hokkaido Imperial University* (6, Zoology) **4**: 115-120.
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Allozyme analysis of Japanese *Semisulcospira* species (Gastropoda: Pleuroceridae) reveals that Lake Biwa endemic species are not monophyletic*

Satoshi Kamiya¹, Masanori Shimamoto^{2†}, and Takashi Hashimoto³

¹ Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, 6-3 Aoba, Aoba-ku, Sendai 980-8578, Japan

² The Tohoku University Museum, 6-3 Aoba, Aoba-ku, Sendai 980-8578, Japan

³ Nihon M&A Center Inc., 1-8-3 Marunouchi, Chiyoda-ku, Tokyo 100-0005, Japan

Correspondence, Masanori Shimamoto: meteoroid@ma.mni.ne.jp

Abstract: Lake Biwa (Shiga Prefecture, Japan) is an ancient lake with many endemic species. In particular, 15 extant endemic species of the genus *Semisulcospira* (Caenogastropoda: Pleuroceridae) have attracted attention because they may represent a single species flock. Although many taxonomic studies have been conducted on these Lake Biwa species and on non-Biwa species of the genus, their genetic relationships remain unresolved. We use allozyme analysis to investigate the genetic differentiation of 12 species of the genus *Semisulcospira*, including nine Lake Biwa endemics: *S. (Biwamelania) arenicola* Watanabe and Nishino, 1995, *S. (B.) decipiens* (Westerlund, 1883), *S. (B.) fluvialis* Watanabe and Nishino, 1995, *S. (B.) multigranosa* (Böttger, 1886), *S. (B.) nakasekoe* Kuroda, 1929, *S. (B.) ourense* Watanabe and Nishino, 1995, *S. (B.) fuscata* Watanabe and Nishino, 1995, *S. (B.) niponica* (Smith, 1876), and *S. (B.) habei* Davis, 1969, and three non-Biwa species: *S. (S.) libertina* (Gould, 1859), *S. (S.) reiniana* (Brot, 1877), and *S. (S.) kurodai* Kajiyama and Habe, 1961. Based on their genetic features, the Lake Biwa endemics were divided into three groups, the *S. (B.) decipiens* group, *S. (B.) niponica* group, and *S. (B.) habei* group. The observed genotype frequencies of the Lake Biwa endemics within each group were similar to each other. We tested the observed genotype frequencies for each polymorphic locus in each local population of the Lake Biwa endemics for departure from Hardy–Weinberg equilibrium. Most of the eight polymorphic loci of the Lake Biwa populations did not deviate significantly from HWE, except for Aat of *S. (B.) arenicola* at the site B8, Pgm-1 of *S. (B.) fluvialis* at the site B9, and *S. (B.) habei* at the site B1 (level of significance $\alpha = 0.05$). The *S. (B.) niponica* and *S. (B.) habei* groups showed similar genetic features to the non-Biwa *S. (S.) libertina* and *S. (S.) reiniana* groups, whereas the *S. (B.) decipiens* group was distinct from any other group. Our allozyme data suggest that *Semisulcospira* species in Japan are distinguished robustly into two major lineages, the *S. (B.) decipiens* group and a separate non-*decipiens* group, and that all extant Lake Biwa endemics do not form a single species flock, as proposed previously.

Key words: genetic variation, allozymes, Lake Biwa, endemic speciation, *Semisulcospira*

Lake Biwa (Shiga Prefecture, Japan) has endured for about four million years and is recognized as an ancient lake, similar to Lake Tanganyika in Africa and Lake Baikal in Russia. Many endemic species in several taxa—for example, of shrimp, fish, and molluscs—have been reported in Lake Biwa (Mori and Miura 1980), as they have in other ancient lakes. In particular, 15 endemic species of the subgenus *Biwamelania* in the genus *Semisulcospira* (Caenogastropoda: Pleuroceridae) have been investigated because they may represent a single species flock (Nishino and Watanabe 2000). However, the genetic diversity of these Lake Biwa endemics has not been studied adequately. It is important to consider the genetic relationships among the Lake Biwa endemics to understand their speciation pattern during the formation of

the Lake Biwa water system, and to help elucidate the reasons why so many endemic species have been maintained in the lake. In this study, we investigated the genetic variation of Japanese *Semisulcospira* species including nine Lake Biwa endemics, using allozyme analysis.

Davis (1969) studied the taxonomy of Japanese *Semisulcospira* species and divided them into two groups: the *S. libertina* species complex and the *S. niponica* species complex, based on the number of embryos in the female brood pouch, basal cords of adult shells, and chromosomes. The *S. libertina* species complex contains *S. libertina* (Gould, 1859), *S. reiniana* (Brot, 1877), and *S. kurodai* Kajiyama and Habe, 1961, which live in a widely dispersed area outside Lake Biwa. The *S. niponica* species complex consists of six Lake

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† Present address: 3-20-5 Sumiyoshidai-higashi, Izumi-ku, Sendai 981-3222, Japan

Biwa endemic species, *S. niponica* (Smith, 1876), *S. decipiens* (Westerlund, 1883), *S. multigranosa* (Böttger, 1886), *S. reticulata* Kajiyama and Habe, 1961, *S. nakasekoe* Kuroda, 1929, and *S. habei* Davis, 1969. Habe (1978) classified the “*S. niponica* species complex” under the genus *Biwamelania*, and Matsuoka and Nakamura (1981) assigned it to the subgenus *Biwamelania* with *S. niponica* as a holotype. Watanabe (1984) described *S. morii*, which lives only around small islands in Lake Biwa. Watanabe and Nishino (1995) investigated morphological variation in the endemic species and proposed eight new species: *S. fuscata*, *S. dilatata*, *S. rugosa*, *S. ourense*, *S. takeshimensis*, *S. shiraishiensis*, *S. fluvialis*, and *S. arenicola*, classified under the subgenus *Biwamelania*. Moreover, they reported that *S. niponica* contains three morphological types, the *biwae*, *nodose*, and *ribbed* types, based on their shell sculptures. Consequently, it was suggested that many more species than previously thought are endemic to Lake Biwa.

As taxonomical research has improved, variation in shell morphology of *Semisulcospira* species has been clarified. Urabe (1992) studied two sympatric species, *S. libertina* and *S. reiniana*, from the viewpoint of genetic and morphological variation, and determined that they could be divided into two populations having unique homozygous genotypes at the locus *Mpi*: types *Mpi*-A and *Mpi*-B. She also suggested that it is difficult to identify the two species based only on their shell morphology and pointed out the individuals with the *Mpi*-B genotype could be assigned to *S. reiniana*. Recently, Kamiya and Shimamoto (2005) confirmed that the *Semisulcospira* populations with the *Mpi*-A genotype from Tohoku (northern area of Japan) to Kansai District (western area of Japan) correspond to *S. (S.) libertina*, and that the populations having the *Mpi*-B genotype in Kanto (eastern area of Japan) to Kansai District are *S. (S.) reiniana*.

A study of the phylogeny of *Semisulcospira* species was conducted by Oniwa and Kimura (1986). They examined the phylogenetic relationships of six species: *S. (S.) libertina*, *S. (S.) reiniana*, *S. (S.) kurodai*, *S. (B.) niponica*, *S. (B.) multigranosa*, and *S. (B.) nakasekoe*, through allozyme analysis, and noted large genetic differences between the Lake Biwa endemics, *S. (B.) niponica*, *S. (B.) multigranosa*, and *S. (B.) nakasekoe*, and the non-Biwa species, *S. (S.) libertina*, *S. (S.) reiniana*, and *S. (S.) kurodai*. However, the phylogenetic positions of these endemic species remain unsettled.

The fossil record of *Semisulcospira* has been studied by Matsuoka (1987). The fossils of *S. (B.) habei* occur from the Katata Formation (early to middle Pleistocene), and this species is assumed to be the oldest extant species of *Semisulcospira* (Matsuoka 1987). Nishino and Watanabe (2000) presumed that *S. (B.) habei* is a common ancestor of all extant Lake Biwa endemics, and that these endemic

species were derived over a short period of time from *S. (B.) habei*.

We investigated the genetic variation and relationship among nine endemic species of the subgenus *Biwamelania*: *Semisulcospira (B.) niponica*, *S. (B.) decipiens*, *S. (B.) multigranosa*, *S. (B.) nakasekoe*, *S. (B.) fuscata*, *S. (B.) ourense*, *S. (B.) fluvialis*, and *S. (B.) arenicola* in Lake Biwa; and three non-Biwa species of the subgenus *Semisulcospira*, *S. (S.) libertina*, *S. (S.) reiniana*, and *S. (S.) kurodai*, which are widely dispersed outside Lake Biwa. Using allozyme analysis, we found that the endemic species of the subgenus *Biwamelania* can be discriminated into three groups, the *S. (B.) decipiens* group, *S. (B.) habei* group, and *S. (B.) niponica* group. The *S. (B.) habei* and *S. (B.) niponica* groups are closely related with the non-Biwa species *S. (S.) libertina*, *S. (S.) reiniana*, and *S. (S.) kurodai*, whereas the *S. (B.) decipiens* group is significantly different in its genetic features and phylogenetic position.

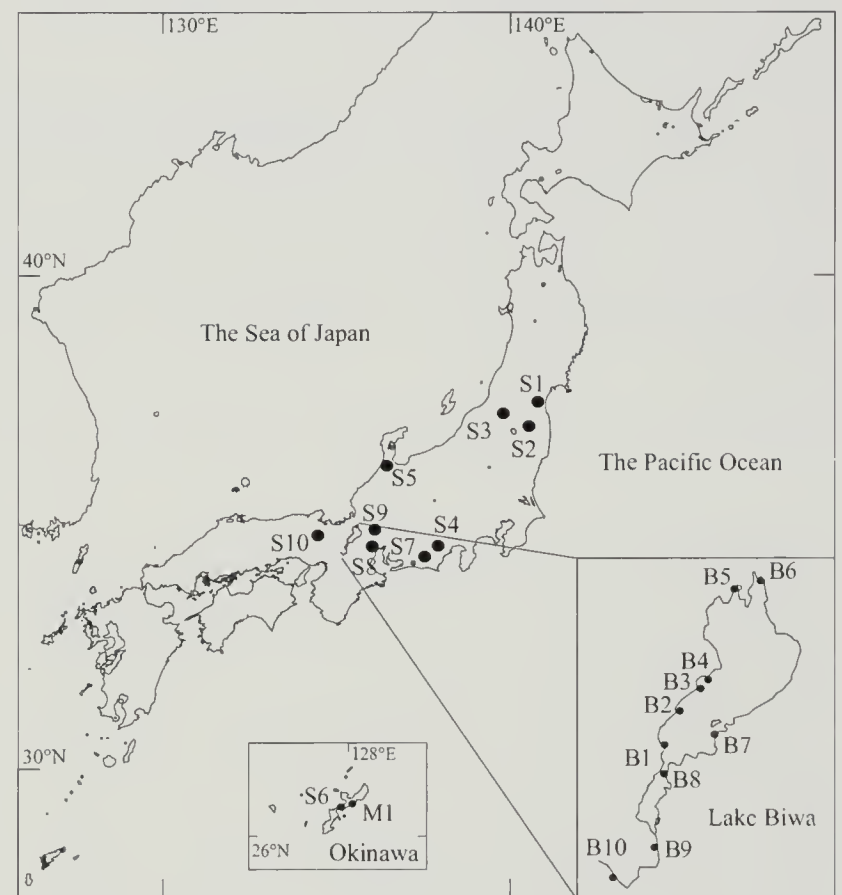


Figure 1. Map of the Japanese Islands indicating sample collection sites. S1, Sendai (Miyagi); S2, Fukushima (Fukushima); S3, Sekikawa (Niigata); S4, Fujieda (Shizuoka); S5, Kanazawa (Ishikawa); S6, On-na (Okinawa); S7, Hamamatsu (Shizuoka); S8, Komaki (Aichi); S9, Takatomi (Gifu); S10, Yoka (Hyogo); B1, Wanihama (Lake Biwa); B2, Omimaiko (Lake Biwa); B3, Shirahigehama (Lake Biwa); B4, Haginohama (Lake Biwa); B5, Oura (Lake Biwa); B6, Hannoura (Lake Biwa); B7, Mizugahama (Lake Biwa); B8, Imahama (Lake Biwa); B9, Nango (Seta River); B10, Uji (Uji River); M1, Nago (Okinawa).